It is possible that dorsal raphe serotonin is not rewarding outright, but may serve to influence processing of real-world rewards. To assess this possibility, the mice performed a task in which they chose to enter one of two wells. Each well was associated with different probabilities of reward as well as different probabilities of serotonin stimulation. These probabilities were varied across blocks' allowing the authors to track choice behavior as a function of reward probability and/or stimulation probability. Only reward probability influenced choice behavior. Dorsal raphe serotonin stimulation did not bias choice behavior in any direction.

Stimulation of dorsal raphe serotonergic neurons that is sufficient to boost patient waiting is insufficient to be rewarding. The finding of a selective role for serotonin in boosting patience is strengthened by recent findings that stimulation of *non-serotonergic* dorsal raphe neurons *is* rewarding [8,9]. Taken together, the results suggest there are separate circuits for patience and reward in the dorsal raphe (Figure 1). Non-serotonergic signals for reward are mediated through projections to ventral tegmental area [8,9]. Candidate regions to implement serotonergic signals for patience are the nucleus accumbens, prefrontal and orbitofrontal cortices [10]. These regions are integral to goal-directed actions [11–13] and receive strong serotonergic input [5].

The need for patience extends well beyond getting your morning coffee. An inability to exercise patience (impulsivity) is a prominent component of attention-deficit/hyperactivity disorder and addiction [14]. By identifying dorsal raphe serotonin neurons as a central node, future studies may rapidly identify a more complete neural circuit for patient waiting.

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Animal Navigation: Memories of Home

Sea turtles memorize the magnetic coordinates of their natal beach, returning to that combination of parameters to lay eggs decades later. The intervening secular (year-to-year) variation in field intensity and inclination can lead the nesting females to a series of predictably different beaches.

James L. Gould

Most long-distance migrants make their initial journey from home flying or swimming solo, often at night [1]. Many return later to their natal area with considerable precision. To accomplish this feat, the young animal is hypothesized to 'imprint' on the nest site, storing navigational information for later use. The subsequent return must depend on some combination of wide-area information and local cues. The basis of the larger-scale ability is that mystery of mysteries in animal navigation, the map sense. In at least the case of loggerhead sea turtles, the global cues for homing after displacement, as well as juvenile orientation to the initial feeding area, are unambiguously magnetic [2,3]. In this issue of *Current Biology*, Brothers and Lohmann [4] now show that the return to the natal area is also based on the precise intensity and inclination of the magnetic field. Remarkably enough, they demonstrated the reality of this long-term navigational memory without tracking a single turtle.

The initial proposal that the animal map is based on magnetic parameters arose from a series of anomalies in the results of homing pigeon research [5]. The earth's magnetic field is aligned with the magnetic poles. At present, the magnetic north pole is displaced by about 500 km from the geographic North Pole. The total intensity of the field increases by about a factor of two from the magnetic equator to the poles.

At the same time, the inclination of the magnetic field changes from 0° (horizontal) at the magnetic equator to 90° (straight down) at the poles. Because the gradients of these two parameters are not aligned, over wide areas the combination of intensity and inclination is unique to each location.

To use a magnetic-map strategy to its fullest, the young animal needs not only to memorize the two key parameters, but also the local gradient of each — both direction and rate of change [1]. This would permit the creature to extrapolate the grid of magnetic coordinates from its home area for use farther afield. (Less elaborately, an animal that knows the values for the two magnetic parameters could find the target using a simple but less efficient getting-warmer strategy; this may be the approach used by long-distance seasonal migrants in their first autumn, where the never-before-visited goal is very localized — a Pacific island, for instance [1].)

Two potential problems are apparent in this scenario. The first is that, on a continental scale, the local grid is less and less predictive of the pattern at distant locations. Any 'imprinting' on the home gradients would need to be updated during later travel, as is well documented for migrants using magnetic direction and star patterns as a compass [1]. The other problem is the secular variation in the magnetic parameters. The earth's field is generated by a semi-chaotic flow of molten iron in the planet's core. The consequence for navigating animals using magnetic compasses and maps alike is well illustrated by the misbehavior of the north magnetic pole: over the past 110 years, it has wandered 1600 km NNW. This changes the declination, total intensity, inclination, and various gradients throughout the northern hemisphere, often in quite non-linear ways. For relatively short-lived birds, this is of little consequence. But a hatchling sea turtle (Figure 1) will not return to nest for 20–30 years, and then at 2–3 year intervals after that for another two or three decades. By this time, the memorized parameters of its natal beach will have drifted several — perhaps dozens of — kilometers from the original nesting site. The exact location may have moved along the coast, or inland, or out to sea.

Figure 1. They'll be back.
Hatchling loggerhead sea turtles excavate themselves from their nest and then head for the ocean, where they will remain for perhaps a quarter of a century before returning to mate and lay eggs. (Photo: Elise Peterson/Wikimedia Commons.)

As computer scientists like to remind us, every 'bug' in a system is in fact a potential 'feature' (G.F. Gould, personal communication). Brothers and Lohmann [4] have performed an extremely clever analysis of 19 years of nesting data along 600 km of the Florida coast, taking initially unpromising data and looking at it in an entirely new way. They have examined records of the change in magnetic parameters for each of 12 counties over 17 individual time intervals, scoring each for the degree and direction of change in strength and inclination. This revealed how the locations of the coordinate values have drifted, sometimes closer together, sometimes further apart. Imagine an idealized original beach (Figure 2, top line) where the parameter in question has been measured at a series of distances along the coast (yielding values a, b, c, and so on). After an interval the non-linear secular variation of the parameter has not only led to a general drift down the beach (Figure 2, bottom line) but also to areas of comparative clustering (red) and dispersal (blue).

Brothers and Lohmann [4] reasoned that, regardless of initial nesting patterns and time since hatching, there should be a trend toward increasing nest density where parameter clustering occurs, and a lower density in parameter-dispersal regions. And what a trend there is: for both total intensity and inclination, the *P*-values are <0.001. This means that despite the many sources of noise, fidelity to magnetic coordinates is extremely strong. Of course, the turtles must have backup strategies available to take over when the magnetic parameters lead them to an unsuitable bit of coast (a mangrove forest, for instance), a piece of open ocean, or a location well inland: they must search for the nearest appropriate beach.

Although this outstanding analysis has demonstrated long-term parameter learning, it does not prove that actual imprinting is taking place. Imprinting is an extreme case of the general process of animal conditioning: programmed learning [6]. True imprinting is characterized by a critical period for learning, the absence of any overt reward, and the irreversibility of the memory. But just as most long-distance navigators are programmed to update and recalibrate their navigational software as they travel, so too it could be that sea turtles only remember the coordinates of the most recent suitable beach they nested on. This would reduce the discrepancy between the remembered

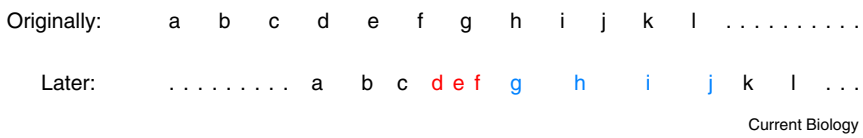

Figure 2. Effect of secular variation on the gradient of a magnetic parameter.

Top line: this idealized beach has, initially, an evenly spaced set of parameter values (intensity or inclination) running from left to right (west to east, say). Bottom line: with the passage of time the locations with these particular parameter values will have drifted in a non-linear way, leading to regions where the values are clumped (red) or dispersed (blue). Nesting density tracks this shift.

geographical location and the one currently designated by the pair of magnetic parameters — a particularly useful update if the apparent target has moved inland. The imprinting/remigration alternatives can only be resolved by tracking individuals, a task that necessarily involves waiting a couple of decades for hatchlings to mature and nest twice — a heroic (and unlikely) undertaking.

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Motor Neuroscience: Changing the Future and Remembering the Past

A new study shows that two skills that would otherwise interfere can be learned if each has a unique following action, and that a single skill is learned more quickly if the goal of the subsequent action is consistent across trials.

Chris Miall

What factors constrain the acquisition and retention of a motor behavior or skill? Many studies explore these issues by measuring the interference caused by learning two incompatible tasks, as a probe of the retention of one motor memory in the face of another competing one. In this issue, Howard *et al.* [1] report that participants can compensate for two different and conflicting perturbations in a reaching task, if a subsequent movement provides a cue to disambiguate the two conditions. This implies that the context in which we learn a skill includes not only current and past actions [2] but also future actions.

Motor skills are learned and refined based on movement outcomes. This process normally combines reinforcement learning, where success is signaled by reward and influences future action choices, and error-correction, where feedback directs performance changes to reduce subsequent errors. Both types of learning depend on a memory trace of a recent action, which can be used to attribute responsibility to the action for any reward or error. These two processes gradually alter the neural representation of the motor actions — often referred to as an internal model [3] — and the improved performance is taken as a measure of acquired 'skill'.

How then is it possible to learn two different but similar skills? Why don't these learning processes degrade existing skills while improving newly learned ones? For example, the leg movements involved in cycling or dancing are not very distinct from those used in walking, and share similar neural control circuits. But luckily we do not forget how to walk when we learn to cycle or dance; in fact locomotor control is so flexible that we can learn direction specific walking patterns in the lab that we would never encounter in our normal environment [4,5]. Other examples abound — tennis and squash, typing and piano playing, and so on.

However, there are also striking counterexamples, in which apparently simple tasks simply don't get learnt. In 2002, Karniel and Mussa-Ivaldi [6] reported that people quickly learn to move a robotic handle to a target despite their arm being perturbed by a lateral force, but if the direction of the force is alternated on every trial, left and right, they just don't learn. This remarkable failure to learn in the face of a simple task can be attributed to the dumb process of error correction: if on one trial the force is leftward, then on the next trial the participant should try to move more towards the right; if this coincides with a reversal of the force field, then moving rightwards makes things worse rather than better, and there is an even bigger overshoot. With less frequent switches, both conditions are learned, albeit slowly, as there are repeated errors under the same condition [7]. If the conditions are presented in blocks, with hundreds of trials with one perturbation before each reversal, participants learn each condition well, but have to repeatedly learn and relearn.

So learning one skill often does block retention of another — the error-corrections in one condition affect the memory of actions established in the previous condition [8]. A contextual cue is then required to allow the two conditions to be separated, so that one is learnt without erasing the other. With cues